Plant and Soil **158**: 29–37, 1994.

PLSO 3111

Plant nutrient efficiency: A comparison of definitions and suggested improvement*

C.J.P. GOURLEY[1], D.L. ALLAN[2] and M.P. RUSSELLE[3]
[1]*Ellinbank Dairy Research Institute, Victorian Department of Agriculture, Warragul South, Victoria, Australia 3820*; [2]*Soil Science Department, 439 Borlaug Hall, University of Minnesota, St. Paul, MN 55108-6028, USA*; [3]*USDA-Agriculture Research Service, 439 Borlaug Hall, University of Minnesota, St. Paul, MN 55108-6028, USA*

Received 16 March 1993. Accepted in revised form 18 August 1993

Key words: alfalfa, *Medicago sativa*, nutrient efficiency, nutrient utilization, phosphorus efficiency, root morphology, sand-alumina, *Trifolium repens*, white clover

Abstract

Selection of plant cultivars tolerant of low nutrient supply may increase productivity on low fertility soils and reduce fertilizer requirements. Considerable effort has been directed towards identifying 'nutrient efficient' species and germplasms, but the many different definitions for efficiency make the use of the term ambiguous. The concept of nutrient efficiency was evaluated using data from a study of differences in germplasm response to phosphorus (P) availability in white clover (*Trifolium repens* L.) and alfalfa (*Medicago sativa* L.) grown in a sand-alumina culture. Application of various criteria identified in the literature as measures of nutrient efficiency did not clarify differences between purportedly P efficient and inefficient germplasms. Germplasms differed in maximum shoot and total dry mass and in solution P concentration required to achieve 80% maximum yield, but not in tissue P concentration, internal P utilization, or P uptake per unit of fine root dry mass. Differences may have resulted from factors other than efficient use of available P. To reduce the confounding effects that other factors have on nutrient efficiency, we propose that *equivalent yields* of germplasms be demonstrated where nutrients are not limiting. Mechanisms that enable enhanced nutrient efficiency can be identified less ambiguously using this improved approach.

Introduction

Exploiting genetic diversity of plants for enhanced productivity in low fertility soils is a desirable, if not an essential, goal, in order to meet food demands for an increasing world population. Diversity among germplasms in the ability to acquire plant nutrients from the environment has been investigated for decades (Lyness, 1936; Godwin and Blair, 1991) and is the subject of many reviews (Blair, 1993, Gerloff, 1976; Gerloff and Gabelman, 1983; Glass, 1989; Saric, 1982). The term 'nutrient efficiency' has been used widely as a measure of the capacity of a plant to acquire and utilize nutrients for production of timber, crops or forages. Definitions of nutrient efficiency vary greatly (Clark, 1990) however, and in some cases may be misleading in the quest for increased productivity and identification of mechanisms for enhanced nutrient acquisition and utilization.

* Joint contribution of the Minnesota Agricultural Experimental Station, USDA-ARS and US Dairy Forage Research Center (Minnesota cluster). Paper No. 20,432 of the Minnesota Science Journal Series.

Definitions of nutrient efficiency generally can be divided into those emphasizing productivity and those emphasizing the internal nutrient requirement of the plant. With regard to yield parameters, nutrient efficiency has been defined as the ability to produce a high plant yield in a soil, or other media, that would otherwise limit the production of a standard line (Buso and Bliss, 1988; Graham, 1984). Other definitions of nutrient efficiency, also referred to as 'agronomic efficiency', include plant production of shoots, or harvestable product, per unit of nutrient applied (Blair and Cordero, 1978; Caradus, 1990; Moll et al., 1987; Saric, 1982; Sauerbeck and Helal, 1990), or 'external P requirement', the amount of nutrient in the media required to achieve a given percentage of maximum yield (Föhse et al., 1988; Fox, 1981; Spencer et al., 1980). Yield response per unit of added nutrient has been used also as a measure of nutrient efficiency (Baligar et al., 1990; Blair, 1993; Thung, 1988).

Alternatively, nutrient efficiency emphasizing utilization is generally defined as total plant biomass produced per unit nutrient absorbed, which is equivalent to the reciprocal of nutrient concentration in the entire plant. This often is called the 'nutrient efficiency ratio' and has been used extensively to describe the internal nutrient requirement in many agronomic species (Baligar et al., 1990; Coltman et al., 1985; Elliott and Läuchli, 1985; Gerloff and Gabelman, 1983; Glass, 1989; Godwin and Blair, 1991; McLachlan, 1976), and also in forest species (Prescott et al., 1989). Using this definition, selection for increased P tissue concentration in alfalfa shoots in an attempt to overcome P nutrition limitations in cattle (Miller et al., 1987), resulted in selection of P inefficient germplasms. Some researchers have used the amount of harvestable product, rather than total plant biomass, per unit of nutrient absorbed (Blair and Cordero, 1978; Buso and Bliss, 1988; Moll et al., 1987).

Siddiqi and Glass (1981) argued that the reciprocal of nutrient concentration does not consider the yield of the crop. They suggested that a more appropriate measure of nutrient efficiency is the product of yield times the reciprocal of nutrient concentration, which they termed 'utilization efficiency'. Other researchers have used 'uptake efficiency', defined as nutrient uptake per unit root length, surface area, or weight, as measures of nutrient efficiency (Blair and Cordero, 1978; Buso and Bliss, 1988; Coltman et al., 1985; Elliott and Läuchli, 1985).

Identification of germplasms or species with differing nutrient efficiencies, by whatever definition, generally includes investigation of potential morphological, physiological, and biochemical mechanisms involved. These mechanisms have been well reviewed (Caradus, 1990; Clarkson and Hanson, 1980; Sauerbeck and Helal, 1988). However, it is often difficult to separate cause from effect when evaluating potential mechanisms of efficient nutrient uptake and utilization. For example, a cultivar with a larger root system is likely to accumulate a greater amount of P and achieve greater yields than a cultivar with a smaller root system (Barber, 1984), but a low cytokinin to auxin ratio may be the reason for the larger root system (Wilkins, 1984). In some cases, specific mechanisms of nutrient uptake have been correlated with plant growth rates. These include rate of nutrient uptake across cell membranes, exudation of organic compounds from the roots and induced pH changes of the rhizosphere, both of which may increase nutrient availability, and the incidence of vesicular-arbuscular mycorrhizal associations (Caradus, 1990; Glass, 1989).

The close relationship between root and shoot activities may mean that differences in yield or nutrient accumulation by plants, resulting from differences in metabolic activity, are incorrectly attributed to differences in root morphology and function. To overcome this problem, Gerloff and Gabelman (1983) proposed that germplasms differing in yields under nutrient stress could only be designated efficient or inefficient if they are normal in appearance and have similar yields when an optimal amount of the nutrient is available (Fig. 1). This constraint has not been widely adopted by researchers and comparisons of nutrient efficiency are often made among species and cultivars with markedly different genetic potentials.

The objectives of this study were: (1) to compare two germplasms of the forage legumes alfalfa and white clover over a range of P rates, using five commonly used definitions of nutrient efficiency; and (2) to recommend appropriate

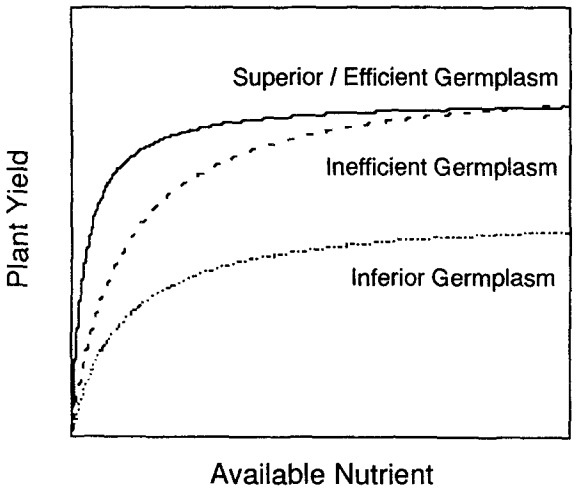

Fig. 1. Hypothetical yield response curves of three germplasms differing in nutrient efficiency and yield potential.

criteria by which efficient and inefficient germplasms can be separated, so that mechanisms which enable enhanced nutrient efficiency can be identified and evaluated less ambiguously.

Methods and materials

Growth conditions

Comparisons were made between two alfalfa germplasms, a 'low P tolerant' (EG2) and 'low P intolerant' (IG2) second generation progeny of 'Rangelander', selected in nutrient solution (Sain, 1990), and two white clover cultivars, which were purportedly P efficient (Gandalf) and moderately efficient (Huia) (J.R. Caradus, pers. comm.). Plants were grown in sand-alumina media (Gourley et al., 1993b) with steady-state solution P concentrations of 0, 2.9, 6.9, 40 and 88 μM. Sixteen surface-sterilized and germinated seeds of each germplasm were sown in 3 kg of the sand-alumina media placed in 15 cm diam. black polyvinylchloride pots and later thinned to four plants per pot. Seedlings were inoculated 5 d after sowing with appropriate strains of *Rhizobium* grown on yeast extract mannitol medium. Each genotype and solution [P] treatment was replicated three times. Pots were watered daily with either 250 or 500 mL of nutrient solution containing: (mM) 3.75 K, 1 Mg, 2 Ca, 4.5 S, 0.128 Na, 0.49 N (as NO_3^-), 0.79 Cl; and (μM) 68 Fe (as Fe^{3+}EDTA), 33 B, 7.4 Mn, 0.94 Zn, 1.5 Mo, and 1 Cu. Solution pH was adjusted to 6.5 with 0.1 M NaOH. Plants were grown in a glasshouse with supplementary lighting provided by high-pressure sodium bulbs (185 to 380 μmol photons m^{-2} s^{-1}) on a 14/10-h day/night cycle and daytime air temperatures of about 27 °C, for 52 days.

At harvest plants were carefully removed from the sand-alumina and separated into herbage, fine roots (<2 mm diam.), and coarse roots (> 2 mm diam.). Plant tissue was dried at 65 °C, weighed, and ground. Phosphorus concentrations of tissue were determined by the vanadomolybdate yellow method (Jackson, 1958), after digestion with H_2SO_4 and 30% H_2O_2 (Thomas et al., 1967). Phosphorus concentration per unit total plant dry mass was calculated from yields and [P] of the different plant parts.

P efficiency indexes

The measures of P efficiency used in this study to assess differences between germplasms were shoot dry mass response curves, external P requirements, P efficiency ratios, P utilization efficiencies, and P uptake efficiencies.

Shoot dry mass response curves for each germplasm were derived from the relationship between shoot dry mass (g pot^{-1}) and solution P (μM), using the Michaelis-Menten equation:

$$\text{Shoot dry mass} = (\alpha \times \text{solution[P]})/(\beta + \text{solution[P]})$$

where α and β were estimates of maximum shoot dry mass and solution [P] at half maximum shoot dry mass, respectively. Of several regression models, this equation provided the best fit of our data (Gourley et al., 1993a). Derived regression models for each germplasm were tested for invariance (Ratkowsky, 1983) to determine whether the two response curves were significantly different ($p < 0.05$). The external P requirement of the four germplasms was determined as the solution [P] required to produce 80% of predicted maximum shoot dry mass

(Föhse et al., 1988) using the derived response curve for each germplasm. The selection of 80% rather than the more commonly used 95% value of maximum shoot dry mass enables differences in solution [P] between the germplasms to be more easily determined.

The following measures of P efficiency were determined at P concentrations of 2.9, 6.9, 40 and 88 μM. Total P accumulation was calculated from total plant dry mass and tissue [P]. Phosphorus efficiency ratio was calculated as total plant dry mass divided by total P accumulation (Gerloff and Gabelman, 1983). Phosphorus utilization efficiency was calculated as total plant dry mass divided by tissue [P] (Siddiqi and Glass, 1981). Phosphorus uptake efficiency (Elliott and Läuchli, 1985) was calculated from total P accumulation divided by fine root dry mass. Fine root dry mass was used rather than total root dry mass because of the greater contribution of fine roots to P uptake (Barber, 1984). Phosphorus concentration of tissue, efficiency ratios, utilization efficiencies, and uptake efficiencies were analyzed by one-way analysis of variance at P concentrations of 2.9, 6.9, 40, and 88 μM to determine statistical differences between germplasms ($p < 0.05$). All statistical analyses were carried out using the computer program 'Systat' (Wilkinson, 1989).

Results

The response curves of shoot dry mass and solution [P] were significantly different ($p < 0.01$) for the alfalfa germplasms EG2 and IG2, and the white clover cultivars Gandalf and Huia (Fig. 2). EG2 had a predicted maximum shoot yield of 4.40 g/pot compared with 3.17 g/pot for IG2. Gandalf had a predicted maximum shoot yield of 4.43 g/pot compared with 2.14 g/pot for Huia. Response curves for total plant dry mass and solution [P] were also significantly different ($p < 0.01$), with predicted maximum total plant dry mass of 5.78 and 3.99 g/pot for EG2 and IG2 and 5.60 and 2.80 g/pot and for Gandalf and Huia, respectively. External P requirement to produce 80% of predicted maximum shoot dry mass was 19 and 32 μM for EG2 and IG2, and

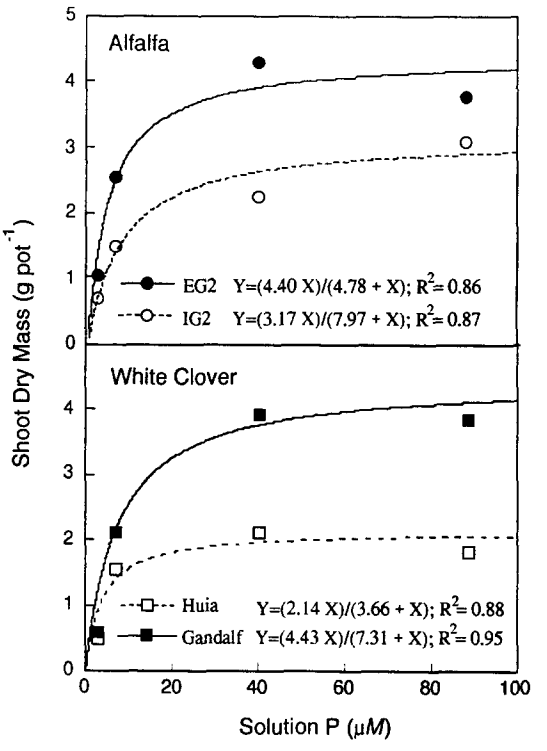

Fig. 2. Shoot dry mass response curves for alfalfa and white clover germplasms over a range of solution P concentrations.

15 and 29 μM for Huia and Gandalf, respectively (Fig. 2).

Plant tissue [P] increased with increasing solution [P], with white clover germplasms having a much higher tissue [P] than the alfalfa germplasms at equivalent solution [P] (Fig. 3). There were no differences in tissue [P] between EG2 and IG2 at any solution [P]. The tissue [P] of Huia was significantly higher than Gandalf at the highest solution [P] of 88 μM, but there were no differences at lower P levels (Fig. 3). At solution concentrations of 40 and 88 μMP, both white clover germplasms had clearly achieved maximum yields (Fig. 2), and it appeared that Huia was accumulating luxury levels of P in plant tissue at the higher solution [P].

Because P efficiency ratio (g DM mg^{-1} P) is equivalent to the reciprocal of tissue [P], differences in P efficiency ratio between germplasms corresponded to differences in tissue [P]. Phosphorus efficiency ratio declined with increasing solution P concentrations, indicating a decline in the internal utilization of P to produce dry mass

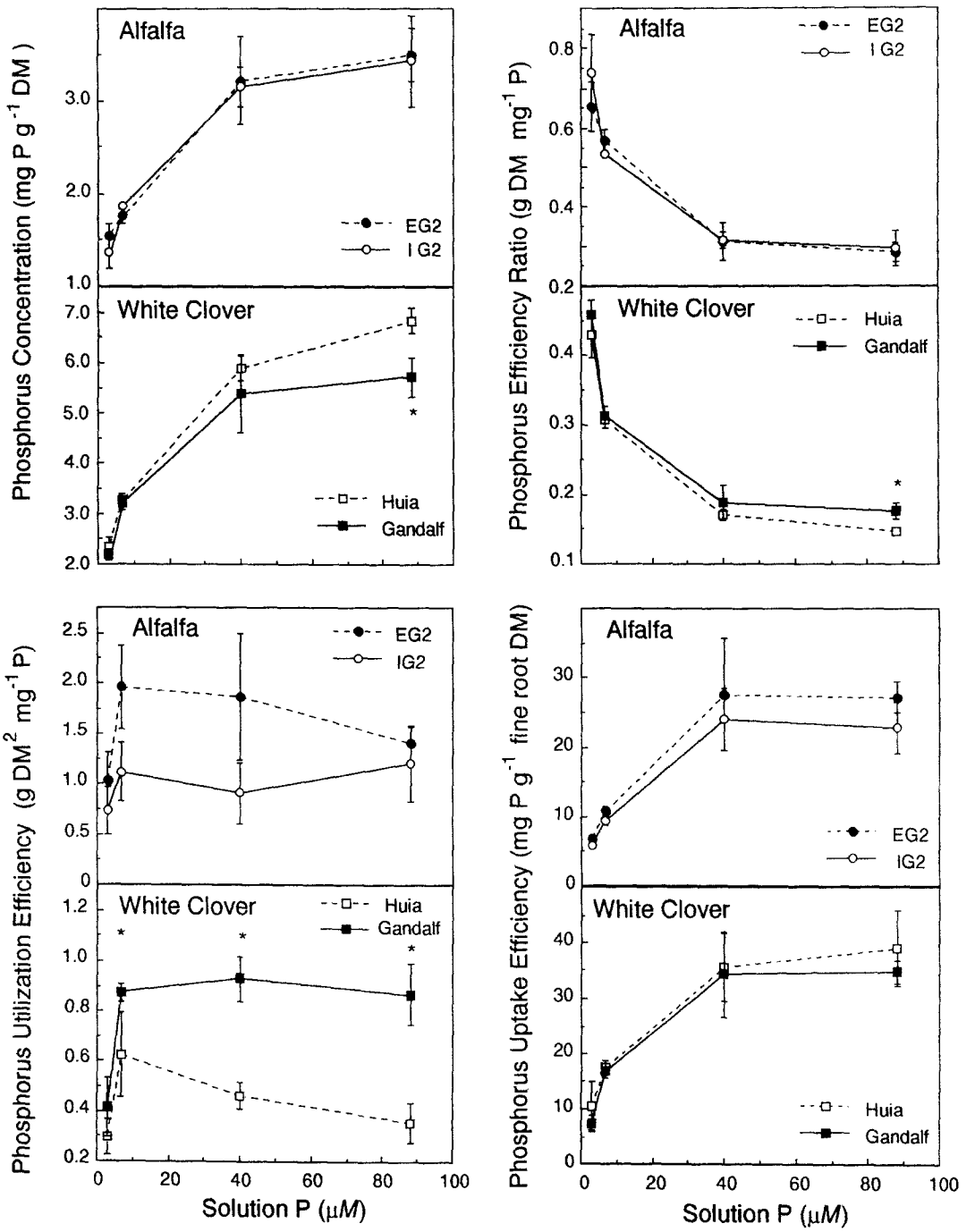

Fig. 3. Plant P concentration, phosphorus efficiency ratios, utilization efficiency and uptake efficiency for alfalfa and white clover germplasms over a range of solution P concentrations. An asterisk indicates that cultivars were significantly different at that solution P concentration ($p < 0.05$). Error bars show SD of the mean.

(Fig. 3). Calculated phosphorus efficiency ratios for EG2 and IG2 were not significantly different at any solution [P], and Gandalf had a significantly higher P efficiency ratio than Huia only at the highest solution [P] (Fig. 3). The ratio of shoot dry mass to total P accumulation provided

parallel results to P efficiency ratio (data not shown).

Utilization efficiency, equal to total dry mass per tissue [P] (with the unusual units of g DM^2 mg^{-1} P), was not significantly different between EG2 and IG2 at any solution [P], despite the trend apparent in Figure 3. There were large standard deviations associated with the mean utilization efficiency value for the alfalfa germplasms. The white clover cultivar Gandalf had a significantly higher utilization efficiency than Huia at solution [P] of 6.9 μM and above (Fig. 3).

Phosphorus uptake efficiency was calculated as total P accumulation divided by fine root dry mass, which provides an average value integrated over the entire plant growth period. There were no significant differences between EG2 and IG2, or between Gandalf and Huia in P uptake efficiency (Fig. 3), indicating that the roots of each germplasm had a similar ability to absorb P from the solution.

Discussion

Comparison of different definitions of nutrient efficiency

These results indicate that different measures of nutrient efficiency can be obtained from the same experimental data, and supports the conclusions of others that ranking species and germplasms for nutrient efficiency can vary according to the definition used (Blair and Cordero, 1978; Föhse et al., 1988; Kemp and Blair, 1991; McLachlan, 1976; Siddiqi and Glass, 1981).

Measuring nutrient efficiency in terms of relative yield (in this case, shoot dry mass) at low P levels, or yield per unit of available P, suggests that EG2 was more P efficient than IG2, and Gandalf was more efficient than Huia. Another yield-based definition, external P requirement, also indicated that EG2 required less solution [P] to achieve 80% of maximum yield than IG2 and was therefore more efficient than IG2, but in contrast indicated that Huia was more efficient than Gandalf. Both these approaches require that a well defined response curve for each germplasm has been determined so that a maximum yield and the rate at which the maximum is achieved can be estimated. This can be assessed accurately only over a wide range of available nutrient, with several data points at lower concentrations to accurately define the shape and slope of the response curve, and with a highest rate equal to or greater than that required to achieve a maximum response. In retrospect, our experiment could have been improved by the addition of several intermediate solution P concentrations (Fox et al. 1986).

Calculations of P efficiency ratio indicated little difference in P efficiency between EG2 and IG2, or between Gandalf and Huia, due to the very similar tissue [P] values of the germplasms. The difference in P efficiency ratio at 88 μM P between Huia and Gandalf is unlikely to be important as differences are most beneficial at low levels of available P (Gerloff and Gabelman, 1983) and is most likely due to luxury uptake of P by Huia. The similarity in tissue [P] within the two alfalfa and two white clover germplasms in this experiment also means that differences in P utilization efficiency were largely due to differences in yields.

The higher yielding germplasms had higher fine root dry mass and also higher total P accumulation than the lower yielding germplasms, which resulted in similar P uptake efficiencies between the germplasms assessed in this study. Greater P accumulation by EG2 and Gandalf was most likely a result of a larger root surface area for P absorption (Barber, 1984; Clarkson and Hanson, 1980). Differences in root hair characteristics between germplasms are unlikely, as there were no differences in root hair density and length between EG2 and IG2, or between Huia and Galdalf, when grown in a low P soil (Gourley, 1993a). The slightly higher P uptake efficiency of EG2 at all solution [P] (Fig. 3) may have resulted from its faster growth rate (Glass, 1989), although Huia also appeared to have a slightly higher P uptake efficiency at 88 μM P but had substantially lower yields than Gandalf.

In summary, the alfalfa germplasm EG2 was significantly more P efficient than IG2 when efficiency was defined as shoot yield or external P requirement, but there was no difference in P efficiency ratio, P utilization efficiency, and P

uptake efficiency between the germplasms. The white clover cultivar Gandalf was more P efficient than Huia, when efficiency was defined as shoot yield or P utilization efficiency, but Huia had a greater P efficiency than Galdalf based on external P requirement. There was no difference between Gandalf and Huia in P efficiency ratio or P uptake efficiency.

Criteria for determining nutrient efficient germplasms

Screening germplasms for shoot dry mass or harvestable product in low P conditions may provide the best estimate of productivity in low P soils, and Gandalf and EG2 would therefore be the preferred germplasms over Huia and IG2. However, before germplasms can be categorized as 'P efficient' or 'P inefficient', it is important to identify whether the superior performance in low P conditions results from one or more specific mechanisms associated with P accumulation or utilization. Many plant metabolic activities, such as phytohormone production, photosynthetic rate, photoperiodism, and production of ATP, can increase nutrient uptake and utilization by influencing root morphology and function (Wilkins, 1984). A greater overall genetic potential, regardless of the mechanism, is likely to result in higher yields *independent* of nutrient availability.

In order to reduce the likelihood that differences in nutrient uptake are due to factors other than those mechanisms specifically associated with nutrient acquisition and utilization, it is essential that germplasms achieve similar yields when optimum amounts of the nutrient are available (Fig. 1). Differences in nutrient efficiency then can be related to the rates at which the maxima are achieved; therefore well defined response curves are required for differences to be determined. Two of the previously discussed definitions, yield at low nutrient availability and external nutrient concentration required to achieve a percentage of maximum yield, both enable the designation of efficient and inefficient germplasms, as long as similar yield maxima are obtained. If the same maximum yield is not achieved, factors other than the nutrient under study are likely to be influencing plant growth.

Only when the two criteria of (a) equal yield at non-limiting nutrient availability and (b) differences in the rate at which maximum yields are achieved, are met, is it appropriate to consider the mechanisms involved in nutrient uptake and acquisition. A truely efficient germplasm could require less nutrient than an inefficient germplasm for normal metabolic processes. The use of nutrient efficiency ratios may therefore indicate a potential mechanism for enhanced nutrient efficiency. For example, Gerloff (1976) attributed greater efficiency ratios to greater yields of field beans (*Phaseolus vulgaris* L.) at low concentrations of K, as opposed to greater K uptake. The calculation of utilization efficiency includes, however, both yield and plant nutrient concentration, and is likely to complicate the identification of potential mechanisms associated with enhanced nutrient efficiency. Differences among germplasms in nutrient uptake per unit root dry mass or length, or differences in root morphological characteristics such as shoot:root ratio or root fineness, may also indicate mechanisms for increased nutrient acquisition at low nutrient availabilities (Caradus, 1990), but do not by themselves identify nutrient efficient or inefficient germplasms.

An example of a specific mechanism that increases P efficiency was provided by Bolan et al. (1983). Formation of vesicular-arbuscular mycorrhizal association with subterranean clover (*Trifolium subterraneum* L.) increased the efficiency of P uptake and yields at low levels of P while similar yields are obtained between inoculated and uninoculated plants when adequate P is available (Fig. 4).

Our results and those from cited literature clearly indicate the importance of establishing sound criteria before designating plant germplasms as nutrient efficient or inefficient and before associating efficiency with particular physiological and morphological characteristics. Similar yields at non-limiting nutrient availability should reduce the possibility that differences in nutrient uptake are due to factors other than those associated with nutrient efficiency. The germplasms assessed in this study should not be described as differing in P efficiency because they differed in maximum yields when P supply was non-limiting. The germplasms are better characterized as superior (EG2 and Gandalf)

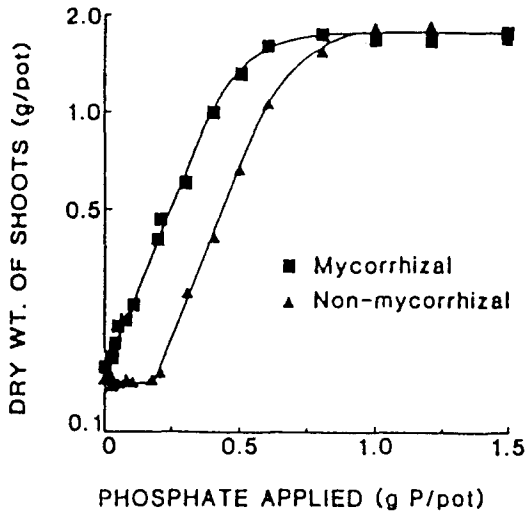

Fig. 4. Example of mechanism which increases phosphorus efficiency. Shoot dry mass response curves for subterranean clover with or without inoculation with mycorrhizae. From Bolan et al. 1983, Fig. 1b.

and inferior (IG2 and Huia) under the growing conditions of this experiment.

Acknowledgements

The authors gratefully acknowledge technical support from W Amossa, J Filson and J White. The senior author was partially funded by the Australian Dairy Research and Development Corporation.

References

Barber S A 1984 Soil Nutrient Bioavailability. John Wiley and Sons, New York.

Baligar V C, Duncan R R, and Fageria N K 1990 Soil-plant interactions on nutrient use efficiency in plants. *In* Crops as Enhancers of Nutrient Use. Eds. V C Baligar and R R Duncan. pp 351–373. Academic Press, San Diego.

Blair G L 1983 Nutrient efficiency – what do we really mean? *In* Genetic Aspects of Plant Mineral Nutrition. Eds. P J Randall, E. Haize, R A Richards and R Munson. pp 205–213. Kluwer Academic Publishers, Dordrecht.

Blair G J and Cordero S 1978. The phosphorus efficiency of three annual legumes. Plant and Soil 50, 387–398.

Bolan N S, Robson A D and Barrow N J 1983 Plant and soil factors including mycorrhizal infection causing sigmoidal response of plants to applied phosphorus. Plant and Soil 73, 187–201.

Buso G S C and Bliss F A 1988 Variability among lettuce cultivars grown at two levels of available phosphorus. Plant and Soil 111, 67–73.

Caradus J R 1990 Mechanisms improving nutrient use by crop and herbage legumes. *In* Crops as Enhancers of Nutrient Use. Eds. V C Baligar and R R Duncan. pp 253–311. Academic Press, San Diego.

Clark R B 1990 Physiology of cereals for mineral nutrient uptake, use and efficiency. *In* Crops as Enhancers of Nutrient Use. Eds. V C Baligar and R R Duncan. pp 131–209. Academic Press, San Diego.

Clarkson D T and Hanson J B 1980 The mineral nutrition of higher plants. Annu. Rev. Plant Physiol. 31, 239–298.

Coltman R R, Gerloff G C and Gabelman W H 1985 Differential tolerance of tomato strains to maintained and deficient levels of phosphorus. J. Am. Soc. Hortic. Sci. 110, 140–144.

Elliott G C and Läuchli A 1985 Phosphorus efficiency and phosphate-iron interactions in maize. Agron. J. 77, 399–403.

Föhse D, Claassen N and Jungk A 1988 Phosphorus efficiency of plants. Plant and Soil 110, 101–109.

Fox R L 1981 External phosphorus requirements of crops. *In* Chemistry in the Soil Environment. Eds. R H Dowdy, J A Ryan, V V Volk and D E Baker. pp 223–239. Spec. Publ. No. 40. American Society of Agronomy and Soil Science Society of America, Madison.

Fox R L, Saunders W M H and Rajan S S S 1986 Phosphorus nutrition of pasture species: phosphorus requirement and root saturation values. Soil Sci. Soc. Am. J. 50, 142–148.

Gerloff G C 1976 Plant efficiencies in the use of nitrogen, phosphorus, and potassium. *In* Plant Adaptation to Mineral Stress in Problem Soils. Ed. M J Wright. pp 161–173. Proc. Workshop Plant Stress Laboratory, USDA. Nov. 1976. Beltsville.

Gerloff G C and Gabelman W H 1983 Genetic basis of inorganic plant nutrition. *In* Encyclopaedia of Plant Physiology. Eds. A Läuchli and R L Bieleski. pp 453–480. New series vol. 15B. Springer Verlag, New York.

Glass A D M 1989 Physiological mechanisms involved with genotypic differences in ion adsorption and utilization. Hort. Sci. 24, 559–564.

Godwin D C and Blair G J 1991 Phosphorus efficiency in pasture species. V. A comparison of white clover accessions. Aust. J. Agric. Res. 42, 531–540.

Gourley C J P, Allan D L and Russelle M P 1993a Differences in response to available phosphorus among white clover cultivars. Agron. J. 85, 296–301.

Gourley C J P, Allan D L, Russelle M P and Bloom P R 1993b Evaluation and improvements of a sand-alumina culture technique to screen plants for low phosphorus tolerance. Soil Sci. Soc. Am. J. 57, 103–110.

Graham R D 1984 Breeding characteristics in cereals. pp. 57–90. *In* Advances in Plant Nutrition, Vol. 1. Eds. P B Tinker and A Läuchli. Praeger, New York.

Jackson M L 1958 Soil Chemical Analysis. Prentice-Hall, Englewood Cliffs. pp 162–165.

Kemp P D and Blair G J 1991 Phosphorus efficiency in pasture species, VI: A comparison of Italian ryegrass,

phalaris, red clover, and white clover over time. Aust. J. Agric. Res. 42, 541–558.

Lyness A S 1936 Varietal differences in the phosphorus feeding capacity of plants. Plant Physiol. 11, 665–686.

McLachlan K D 1976 Comparative phosphorus responses in plants to a range of available phosphorus situations. Aust. J. Agric. Res. 27, 323–341.

Miller D, Waissman N, Melton B, Currier C and McCaslin B 1987 Selection for increased phosphorus in alfalfa and effects on other characteristics. Crop Sci. 27, 22–26.

Moll R H, Kamprath E J and Jackson W A 1987 Development of nitrogen-efficient prolific hybrids of maize. Crop Sci. 27, 181–186.

Prescott C E, Corbin J P and Parkinson D 1989 Biomass, productivity, and nutrient-use efficiency of above ground vegetation in four Rocky Mountain coniferous forests. Can. J. For. Res. 19, 309–317.

Ratkowsky D A 1983 Nonlinear Regression Modeling. A Unified Practical Approach. Marcel Dekker, New York.

Sain S L 1990 Bidirectional selection for phosphorus efficiency in alfalfa using hydroponic whole plant and callus tissue culture screening techniques. Ph D dissentation, University of Minnesota.

Saric M R 1982 Theoretical and practical approaches to the genetic specificity of mineral nutrition of plants. *In* Genetic Specificity of Mineral Nutrition of Plants. Ed. M R Saric. pp 9–20. Proc. Int. Symp. Belgrade.

Sauerbeck D R and Helal H M 1990 Factors affecting the nutrient efficiency of plants. *In* Genetic Aspects of Plant Mineral Nutrition. Eds. N El Bassam, M Dambroth and B C Loughman pp 11–16. Kluwer Academic Publishers, Dordrecht.

Siddiqi M Y and Glass A D 1981 Utilization Index: A modified approach to the estimation and comparison of nutrient utilization efficiency in plants. J. Plant Nutr. 4, 289–302.

Spencer K, Govaars A G and Hely F W 1980 Early phosphorus nutrition of eight forms of two clover species, *Trifolium ambiguum* and *T. repens*. N.Z. J. Agric. Res. 23, 457–475.

Thomas R L, R W Sheard and J R Moyer 1967 Comparison of conventional and automated procedures for nitrogen, phosphorus, and potassium analysis of plant material using a single digest. Agron. J. 59, 240–243.

Thung M 1988 Phosphorus: A limiting nutrient in bean (*Phaseolus vulgaris* L.) production in Latin America and field screening for efficiency and response. *In* Genetic Aspects of Plant Mineral Nutrition. Eds. N El Bassam, M C Dambroth and B C Loughman. pp 501–521. Kluwer Academic Publishers, Dordrecht.

Wilkins M B 1984 Advanced Plant Physiology. John Wiley and Sons, New York.

Wilkinson L 1989 SYSTAT: The Sytem for Statistics. SYSTAT, Evanston.

Section editor: H Lambers